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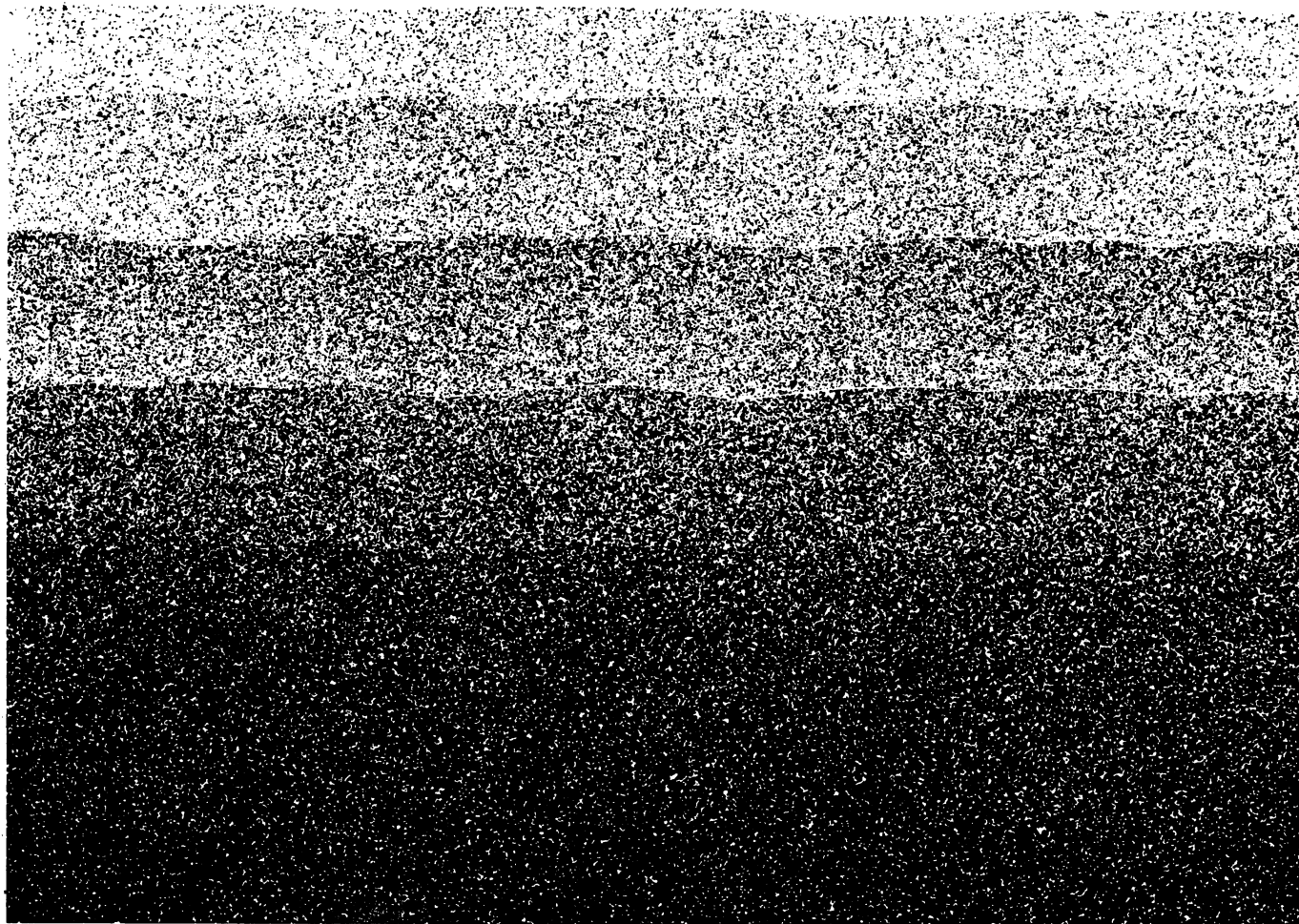
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RATES OF FOREST FLOOR DECOMPOSITION AND NUTRIENT TURNOVER IN ASPEN, PINE, AND SPRUCE STANDS ON TWO SOILS

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Tree nutrition—that is, nutrient uptake, retention, and return in litterfall—is fundamentally distinct from the nutrition of annual agronomic crops. The conservation of nutrients in forests by intracycling provides an important portion of annual nutrient demand. In part, it allows good forest growth on soils that would be poor or unsuitable for agriculture.

But before nutrients returned in litterfall can again be available to trees, they must be mineralized. Nutrients, especially large amounts of K, are made available to some degree through direct leaching. The remaining nutrients are mineralized largely by biological activity—soil micro-organisms, soil animals, and saprophytic plants utilize the organic matter directly as an energy source in their metabolism. Mineral nutrients are eventually released in plant available forms upon the death of the micro-organisms and their predators, or in their waste products. Nitrogen in organic matter is transformed by many biological processes and some becomes available to plants during the nitrogen cycle (Swift *et al.* 1979).

Since the metabolic rate of soil organisms depends on temperature, moisture, pH, and aeration, rates of forest floor decomposition and nutrient turnover vary with environment. The nature and quality of the litter (ease of breakdown) are also important; these vary among tree species, and particularly between conifers and hardwoods (Swift *et al.* 1979).

While many researchers have reported decomposition and nutrient turnover rates for individual forest stands (Olson 1963, Cole and Johnson 1978, Krause *et al.* 1978, Lousier and Parkinson 1976), comparisons among species on the same soil type are rare. Yount (1975) compared white pine and hardwoods on the Coweeta Watershed, but species comparisons

replicated on more than one soil are, to our knowledge, nonexistent. In this paper, we will present estimates of forest floor organic matter decomposition and nutrient turnover rates for trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench.) Voss), red pine (*Pinus resinosa* Ait.), and jack pine (*P. banksiana* Lamb.) growing on two soils of somewhat different site quality.

STUDY AREA

The study area is located on the Chippewa National Forest in north central Minnesota, U.S.A. (47° 20' N, 94° 30' W), in the spruce-fir forest ecoregion (Bailey 1980). The climate is humid warm-summer continental, with cold winters. Annual temperature and precipitation average 4°C and 610 mm.

Both soils occur on a gently undulating till plain. One soil is a Warba very fine sandy loam (Glossic Eutroboralf), well drained, with pH of 5-6 above the calcareous C horizon. The other soil is an unnamed loamy fine sand (Arenic Eutroboralf) underlain at 80 cm by calcareous loam, well drained, with pH of 5-6 in the solum.

About 8 ha were cleared on each soil in either 1933 (loam) or in 1934 (sand), and 0.4 ha adjoining plantations were planted in the autumn of 1933 and 1934 with red pine, jack pine, or white spruce. An unplanted control area on the loam developed through suckering into a fully stocked, even-aged aspen stand. No such control area was established on the sand, but an adjacent two-aged (years of origin 1918 and 1926) aspen stand was available for study instead.

Forty-four species in the shrub and herb layers were present on both soils, most commonly *Corylus cornuta* Marsh., *Lonicera canadensis* Marsh., *Aster*

Table 1.— Stand overstory characteristics

Stand	Soil ¹	Age	Trees/ ha	Mean height	Mean d.b.h. o.b.	Basal area	Biomass	50 year site index
		Yrs.	Number	m	cm	m ² /ha	t/ha	m
Aspen	L	40	2,989 ²	20.3 ³	18 ³	41.7 ²	205 ²	21.9 ³
	S	49	1,237 ²	19.8 ³	24 ³	36.8 ²	211 ²	21.4 ³
Spruce	L	39	2,187	14.4	15	41.1	185	19.7
	S	41	2,718	13.7	14	44.9	179	18.6
Red pine	L	39	1,780	17.6	19	51.9	243	20.7
	S	41	2,364	16.9	16	49.2	200	19.6
Jack pine	L	39	1,580	18.4	17	35.1	175	21.7
	S	41	1,236	19.3	18	30.4	150	21.6

¹L = loam, S = sand.²Includes middle-story hardwoods.³Aspen only.

macrophyllus L., *Maianthemum canadense* Desf., and *Thalictrum dioicum* L. Sixteen species were found exclusively on the sand, including *Vaccinium myrtilloides* Michx., *Rubus strigosus* Michx. and *Streptopus roseus* Michx., and 15 were exclusive to the loam, most notably *Acer saccharum* Marsh., *Tilia americana* L., and *Actaea rubra* (Ait.) Wild. The stand tree characteristics at the time of sampling are given in table 1. More detailed descriptions of the soils and study areas can be found in Alban *et al.* (1978) and Perala and Alban (1982).

METHODS

In early September 1972 (loam soil) and 1974 (sand), ten 4-m² circular understory sampling plots were systematically located in each stand. All herbaceous vegetation was clipped at the ground line to determine biomass and nutrient content (Alban *et al.* 1978). Herbaceous vegetation was inventoried in this manner because it could not be accounted for in litterfall from the tree and shrub layers.

From August 1, 1974, to August 1, 1976, four 1-m² litter traps were systematically located (in stands of each species) on each soil. Litter collections were made five or seven times a year, concentrating in the autumn during maximum litterfall. For purposes of analysis, samples were composited into two sample periods: August to November, and November to August; but only annual averages are reported here.

Forest floor samples were collected with 930 cm² metal frames from 40 locations per stand in October 1972 (loam) and July 1974 (sand). To ease the analytical load, forest floor samples were composited in the field to give 10 samples (loam) and 8 samples (sand).

Samples of litter, herbs, and forest floor were ground to pass a 20-mesh screen and were all analyzed in the same manner. Carbon was determined by induction furnace (Allison *et al.* 1965) and N by the macro-Kjeldahl method (Bremner 1965). After dry ashing (500°C), Ca, Mg, and K were determined by atomic absorption, and P by the molybdophosphoric blue colorimetric method (Jackson 1958). Organic matter in herbs and litterfall is simply the oven-dry (70°) weight uncorrected for ash; forest floor is corrected for ash.

For the sand, August to November litterfall averages for organic matter, C, and nutrients were added to the forest floor to adjust for differences in forest floor sampling times. Thus the forest floor values represent the period immediately following leaf drop for native deciduous trees. The steady-state exponential decay model of Olson (1963),

$$k = \frac{L}{X_{ss}}, \quad (1)$$

was used to estimate instantaneous fractional loss rates (k) for organic matter, C, and nutrients in forest floor. In this equation, L = annual litterfall weights and X_{ss} = forest floor weights in the steady-state. Half-lives of organic matter, C, and nutrients in the forest floor were estimated from the k values using the equation

$$t = \frac{\ln(0.5)}{-k} = \frac{-0.693}{-k}, \quad (2)$$

rewritten from Olson (1963),

$$\ln(X/X_0) = -kt \quad (3)$$

where t = time (years), and X_0 = original amount of litter organic matter, C, or nutrients, and X = amount remaining.

RESULTS

Depending on species, annual litterfall weights averaged from 6 to 18 percent less on the sand soil than on the loam (table 2). The stands on both soils had less litterfall the second year (herbs not considered since they were sampled in only 1 year), ranging from 7 percent less for aspen to 31 percent less for jack pine. During the 2 years, the ranking by species in total litterfall and in C was red pine > jack pine > spruce > aspen for both soils. All nutrients in spruce and red pine litterfall were less on the sand than on the loam, but this varied in aspen and jack pine. In spite of having the least litterfall weight, aspen had the greatest amount of litterfall P, K, Mg, and, along with spruce, Ca. Spruce and jack pine litterfall had the most N. Carbon was least on the sand for all species.

Overall, organic matter (OM) and C in the forest floor were less on the sand than on the loam (table 3). Aspen had the least forest floor OM and C on both soils, while the conifers were nearly identical. The forest floor on the sand had only 45 to 72 percent of the nutrients found in the forest floor on the loam. The forest floor nutrient levels varied widely among species.

The half-lives of OM, C, and nutrients were shorter on the sand than the loam except for red pine OM and C (table 4). The order of half lives for OM, C, and nutrients in the aspen forest floor was N>Ca>Mg>P>C>OM>K, whereas in the conifers it was generally Ca>N>Mg>P>C>OM>K. Thus, all nutrients, except K, were enriched in the forest floor. The ranking of half-lives among species varied depending on nutrient. Spruce had the longest half-lives for K, Mg, and, along with jack pine, P and Ca.

Table 2.—Organic matter, C, and nutrients in annual litterfall¹
(In kg/ha)

Stand	Soil ²	Organic matter	C	N	P	K	Ca	Mg
Aspen	L	4,382	1,972	40	8.2	24	81	8.7
	S	4,105	1,888	39	8.3	34	64	9.2
Spruce	L	5,727	2,520	54	6.9	16	83	4.8
	S	5,263	2,421	41	5.1	12	60	4.1
Red pine	L	6,916	3,389	46	4.9	19	40	7.0
	S	5,638	2,875	37	3.7	18	26	5.8
Jack pine	L	6,210	2,919	51	4.6	17	45	6.5
	S	5,607	2,467	46	4.8	20	31	5.8

¹Mean of two collection years, plus herbs.

²L = loam, S = sand.

Table 3.—Organic matter, C, and nutrients in forest floor
(In kg/ha)

Stand	Soil ²	Organic matter	C	N	P	K	Ca	Mg
Aspen	L	26,840	13,530	667	60	78	1,081	89
	S	22,890	11,580	467	38	51	586	64
Spruce	L	33,080	17,580	752	61	76	1,398	77
	S	28,070	14,050	517	42	49	781	48
Red pine	L	30,290	15,800	538	40	62	660	65
	S	29,390	14,890	370	26	39	294	43
Jack pine	L	32,750	16,860	689	51	68	770	81
	S	27,560	13,480	486	34	44	391	53

¹L = loam, S = sand.

Aspen had the shortest half-lives for P, K, Ca, and, along with red pine, Mg. Aspen also had the longest half-lives for OM, and, along with spruce, C and N. Generally, half-lives for jack pine were longer than for red pine.

DISCUSSION

The half-life estimates given here are suitable for comparing gross differences between species-stands and soils (Swift *et al.* 1979), but their absolute values are less reliable for a number of reasons. First, the annual variation in litterfall is tremendous. For example, over a 7-year period, Ebermayer (1876, cited by Alway and Zon 1930) observed nearly a three-fold range in pine litterfall in Bavaria. Second, there can be large yearly and seasonal variation in forest floor weight and nutrients (Yount 1975). Third, nutrients are added to the forest floor from precipitation, through-fall, stemflow, and N-fixation. Fourth, nutrients are retained on exchange sites or by microbial immobilization, and fifth, nutrients are transferred by roots or hyphae. Clearly, the cycling process is enormously complex (Lousier and Parkinson 1976, Swift *et al.* 1979, Yount 1975).

Table 4.—Half-lives of organic matter, C, and nutrients in forest floor
(In years)

Stand	Soil ²	Organic matter	C	N	P	K	Ca	Mg
Aspen	L	4.2	4.8	11.6	5.1	2.3	9.3	7.1
	S	3.9	4.3	8.3	3.2	1.0	6.3	4.8
Spruce	L	4.0	4.8	9.7	6.1	3.3	11.7	11.1
	S	3.7	4.0	8.7	5.7	2.8	9.0	8.1
Red pine	L	3.0	3.2	8.1	5.7	2.3	11.4	6.4
	S	3.6	3.6	6.9	4.9	1.5	7.8	5.1
Jack pine	L	3.7	4.0	9.4	7.7	2.8	11.9	8.6
	S	3.4	3.8	7.3	4.9	1.5	8.7	6.3

¹L = loam, S = sand.

Finally, the assumption of steady-state cannot be entirely substantiated, although there is strong supporting evidence. The forest floor weights reported here for red pine differ little from those of Minnesota stands 44 to 94 years old (Alban 1974) or 100 and 250 years old (Alway and Zon 1930). There are similar comparisons for jack pine up to 55 years old (Alway and Zon 1930). Therefore, the steady-state assumption does not seem to introduce serious error.

In spite of these many uncertainties, the results compare favorably with those of similar studies. Carbon in the forest floor and annual litterfall in these stands was comparable to those in forests of the eastern United States (Olson 1963). The overall range of k (.14-.22) is medium-high according to Olson (1963), and again within the range reported for eastern conifers. In this study, the range of litter and forest floor C values among species and soils is as great as the range among other stands growing across the eastern U.S. The half-lives for OM are as expected; they are longer than for tropical forests and somewhat longer than for other temperate forests, but much shorter than for boreal forests (table 5). Half-life for aspen litter was slightly longer than for aspen leaf litter after 30 months in 3-mm-mesh bags in Alberta, Canada (Lousier and Parkinson 1976).

The half-lives of nutrients in the forest floor (table 4) were considerably longer than those in other temperate and especially tropical forests, but not much different from those in boreal forests (table 5). The exception was the half-life of N, which is generally much longer in boreal forests.

Nutrient turnover (except for K) lagged behind the turnover of organic matter, a universal observation (Swift *et al.* 1979). The many reasons for this were mentioned earlier.

Forest floor nutrients on the relatively nutrient-poor sand soil were recycled more rapidly than on the loam. This compensated somewhat for the lower inherent fertility of the sand and forest productivity was comparable to the more fertile loam soil (table 1). Why turnover rates were higher on the sand is not known. Tappeiner and Alm (1975) found rapid forest floor decomposition when understory plants were present, especially in red pine stands. The greater proportion of nutrient-rich and relatively easily decomposed litter contributed by shrubs and herbs on the sand (Perala and Alban 1982) accounts in part for faster mineralization. However, litter from the tree layer is not known to decompose faster when mixed with understory litter.

Table 5.—*Literature values for half lives of organic matter and nutrients in forest floor*
(In years)

TROPICAL FOREST							
Location or species	Organic matter	N	P	K	Ca	Mg	Reference
Costa Rica	0.29	—	—	—	—	—	Table 7,
Ghana	.15	0.15	0.21	0.10	0.15	—	Cole and
West Indies	.42	.55	.63	.17	.19	—	Johnson
Columbia	.41	.59	—	—	—	—	(1978)
Florida	.53	1.56	—	—	—	—	
BOREAL FOREST							
Jack pine	5.1	7.5	10.0	1.5	2.6	3.7	Table 6,
Black spruce	18.9	43.0	—	—	—	—	Krause <i>et</i>
Balsam fir	9.7	17.3	18.7	7.5	4.0	—	<i>al.</i> (1978)
Aspen	12.3	32.6	8.3	4.9	9.7	8.3	
TEMPERATE FOREST							
White pine	2.5	.86	5.4	.20	3.2	1.2	Yount
Hardwoods	.82	.32	.92	.23	1.2	.61	(1975)
Red pine	8.4	21.3	14.8	8.6	12.2	—	Alway & Zon
Jack pine (age 30)	3.5	7.7	7.3	6.4	5.7	—	(1930)
Jack pine (age 55)	7.7	13.0	11.3	10.0	9.7	—	
Red pine-hazel	2.2	3.3	2.9	2.1	1.7	1.2	Tappeiner &
Paper birch-hazel	1.2	2.3	0.8	0.1	1.0	0.5	Alm (1975)

CONCLUSIONS

This study showed strong indirect effects by tree species and soils on the rate of nutrient turnover in the forest floor. Comparisons with results from other studies indicate that turnover rates of nutrients and organic matter vary widely within the same ecoregion, and even within species. Detailed studies of decomposer organisms and their microenvironment are needed to explain these differences.

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Compares rates of forest floor decomposition and nutrient turnover in aspen and conifers. These rates were generally most rapid under aspen, slowest under spruce, and more rapid on a loamy fine sand than on a very fine sandy loam. Compares results with literature values.

KEY WORDS: Mineralization, nutrient cycling, litterfall, nitrogen, phosphorus, potassium, calcium, magnesium.